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Pelagic harmful algal blooms and climate change: Lessons from nature's experiments with extremes

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ARTICLE INFO

We dedicate this work to Professor Theodore Smayda, known by generations of HAB scientists as Ted, for his insights and generosity to others in unravelling the mysteries of HAB dynamics. He is deeply missed in the world-wide HAB community.

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ABSTRACT

Time series now have sufficient duration to determine harmful algal bloom (HAB) responses to changing climate conditions, including warming, stratification intensity, freshwater inputs and natural patterns of climate variability, such as the El Niño Southern Oscillation and Pacific Decadal Oscillation. Against the context of time series, such as those available from phytoplankton monitoring, dinoflagellate cyst records, the Continuous Plankton Recorder surveys, and shellfish toxin records, it is possible to identify extreme events that are significant departures from long-term means. Extreme weather events can mimic future climate conditions and provide a "dress rehearsal" for understanding future frequency, intensity and geographic extent of HABs. Three case studies of extreme HAB events are described in detail to explore the drivers and impacts of these oceanic outliers that may become more common in the future. One example is the chain-forming diatom of the genus *Pseudo-nitzschia* in the U.S. Pacific Northwest and its response to the 2014-16 northeast Pacific marine heat wave. The other two case studies are pelagic flagellates. Highly potent *Alexandrium catenella* group 1 dinoflagellate blooms (up to 150 mg/kg PST in mussels; 4 human poisonings) during 2012-17 created havoc for the seafood industry in Tasmania, south-eastern Australia, in a poorly monitored area where such problems were previously unknown. Early evidence suggests that changes in water column stratification during the cold winter-spring season are driving new blooms caused by a previously cryptic species. An expansion of *Pseudochattonella* cf. *verruculosa* to the south and *A. catenella* to the north over the past several years resulted in the convergence of both species to cause the most catastrophic event in the history of the Chilean aquaculture in the austral summer of 2016. Together, these two massive blooms were colloquially known as the "Godzilla-Red tide event", resulting in the largest fish farm mortality ever recorded worldwide, equivalent to an export loss of USD$800 million which when combined with shellfish toxicity, resulted in major social unrest and rioting. Both blooms were linked to the strong El Niño event and the positive phase of the Southern Annular Mode, the latter an indicator of anthropogenic climate change in the southeastern Pacific region. For each of these three examples, representing recent catastrophic events in geographically distinct regions, additional targeted monitoring was employed to improve the understanding of the climate drivers and mechanisms that gave rise to the event and to document the societal response. Scientists must be poised to study future extreme HAB events as these natural experiments provide unique opportunities to define and test multifactorial drivers of blooms.

1. Introduction

The world's oceans are experiencing severe environmental and ecological stress from climate change. The near surface layers of the ocean are under the most pressure because they respond more rapidly and strongly to variations in atmospheric conditions, such as warming, relative to deeper waters. For example, the global average warming of the upper 75 m of the ocean from 1971 to 2010 ha s been 0.11 °C per

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decade, decreasing to 0.015 °C per decade at 700 m depth (Rhein et al., 2013). Conditions in the upper ocean are also more sensitive to changes in freshwater input, which influences salinity and vertical stratification (or the ability of surface waters to mix vertically), ocean currents, and ocean biogeochemistry. In the future, the upper ocean is expected to undergo even more significant change as the global climate continues to warm, to include alterations in underwater light fields, the frequency and intensity of upwelling, thermohaline overturning, nutrient cycling from depth, precipitation and storms (Boyd and Doney, 2002). Of the organisms that inhabit the upper ocean, the phytoplankton, including those that cause harmful algal blooms (HABs), will be among the first to respond to changes in ocean conditions. This is because they have rapid generation times and short lifetimes (Irwin et al., 2015) and because their distribution, survival and success are closely controlled by the physical and chemical characteristics of the water masses in which they reside.

Most efforts to better understand how climate change will influence HABs have focused on the effects of increased temperature, a keystone parameter of climate change that is known to directly and indirectly affect phytoplankton in a variety of ways. Temperature influences critical physiological processes in phytoplankton such as potential growth rates, photosynthesis, motility, and nutrient acquisition rates (cf. review by Wells et al., 2015). Increased temperature may alter the phenology and geography of some HABs. For example, seasonal windows of growth for some harmful algae may expand or contract in some regions (e.g., Moore et al., 2009), while other harmful algae may respond by expanding or contracting their geographic range (Gobler et al., 2017; Townhill et al., 2018). Temperature may indirectly affect phytoplankton populations also via changes in zooplankton grazing (Lewandowska et al., 2014) which could dramatically influence phytoplankton community diversity.

Warming of the upper ocean will increase stratification of coastal waters (Hays et al., 2005; Hallegraeff, 2010; Paerl and Scott, 2010), suppressing nutrient exchange via mixing with deeper waters and enhancing light levels in the upper stratified surface layer (Behrenfeld et al., 2006). The subsequent rapid depletion of surface nutrients may favor phytoplankton, including harmful algae, with unique nutrient acquisition strategies. The strategies used by harmful algae to successfully compete under nutrient limiting conditions include mixotrophy, unique trace metal uptake capabilities, elevated 'surge' macronutrient uptake rates, and swimming to areas where nutrients are more available (Smayda, 2010). Changes in the intensity of ocean mixing or stratification, and the associated changes in nutrient availability, will be a central link between climate change and phytoplankton distribution and composition (Hays et al., 2005).

Ultimately, our ability to predict the impacts of climate change on HABs is limited by our skill in replicating future conditions in the laboratory or extrapolating observed responses of HABs in natural systems to past climate conditions, as well as our inability to predict how strain and species plasticity and evolution will alter current traits. The majority of studies have been conducted using a single species to determine the response to a single variable. Controlled culture experiments in the laboratory, in the absence of competition, grazing, and a multitude of other factors that are present in nature, will inevitably yield either different results compared with in situ populations, or similar results but at varying magnitudes. Multi-factorial experiments are critical to gain a more complete picture of the complex environmental regulators of HAB cell success and toxin production; however, these lab experiments are challenging due to the large matrices that are needed (Wells et al., 2015; Griffith and Gobler, **this issue**, 2019). Because of these challenges, multifactorial experiments are the exception and not the norm and few exist to inform models used to project HAB responses to future climate change. As a consequence, growth responses of HAB species determined in ungrazed, monospecific, nutritionally optimal cultures are used in models to evaluate potential range shifts and changes in bloom phenology (e.g., Moore et al., 2011; Gobler et al., 2017). Townhill et al. (2018) offer a different approach that borrows from landscape ecology, using observed occurrences of HAB species in nature to identify relationships with environmental parameters that are climate sensitive. However, extrapolating these relationships beyond the range of parameters observed introduces uncertainty in the projections of future HAB risks.

Convention is to acquire at least 30 consecutive years of monitoring at a site to identify a "climate normal" and link phytoplankton abundance records to environmental variables (Dale et al., 2006). In many regions of the world, sustained HAB species and toxin monitoring now allow for an analysis of long-term trends that provide some evidence for strong climate drivers of HABs over 30+ years. For example, monitoring of HAB toxins in shellfish to protect public health date back to the 1950s in the Pacific Northwest of the U.S. In Puget Sound, an inland fjord in Washington State, increased concentrations in shellfish of paralytic shellfish poisoning (PSP) toxins, produced by dinoflagellate species of *Alexandrium*, covary with warm phases of the PDO; however, no such relationship exists for El Niño events (Moore et al., 2011). In contrast, on the outer coasts of Washington and Oregon, increased concentrations of domoic acid (DA), produced by species of the diatom *Pseudo-nitzschia*, coincide with or closely follow the warm phases of both PDO and ENSO (McKibben et al., 2017; McCabe et al., 2016) but this pattern does not hold for sites further south (Sekula-Wood et al., 2011).

The longest time series, dating back to the 1940s in the North Atlantic, has been collected by the Continuous Plankton Recorder (CPR), a unique platform that is used to monitor large phytoplankton and zooplankton. The frequency and geographical range of the CPR sampling enables samples to be collected over a larger spatial scale to determine whether changes are more localized or widespread. The limitations of CPR data include its collection only of subsurface samples at 4–7 m with poor taxonomic resolution unless techniques such as scanning electron microscopy are employed to confirm species identities. However, the high-throughput nature of sample collection does convey some benefits. Although the CPR was originally designed to collect zooplankton with its ~270 μm mesh, the large volumes of water filtered can contain high densities of phytoplankton that either effectively reduce the mesh size or stick to the microthreads of the silk material (Batten et al., 2003; Stern et al., 2018). Although there are very few HAB genera that can be effectively sampled using the CPR, a recent study has demonstrated its value in characterizing changing temporal and spatial patterns of *Pseudo-nitzschia* species in the North Pacific (Stern et al., 2018). Decades of data from the CPR have also demonstrated the linkage between rising SST and milder winter temperatures with a shift from diatoms to dinoflagellates in the North Atlantic, the North Sea (Edwards et al., 2001; Hickel, 1998) and the Baltic Sea (Wasmund et al., 1998). As many HAB species are dinoflagellates, these data may suggest that earlier and more frequent dinoflagellate HABs may result from both the direct effects of increasing temperature and indirect effects such as warming-induced stratification (Edwards and Richardson, 2004) that will favor swimmers that are able to access light near the surface and macronutrients at depth.

Dinoflagellate cyst records in sediment cores can also be used to reconstruct time series and evaluate relationships with climate drivers. Many dinoflagellates produce a non-motile, resting cyst stage that can be buried and preserved in bottom sediments and entrained into the sedimentary record (Dale, 2001). Enumerating cysts and dating sediment layers enables reconstruction of historical patterns in abundance that may be indicative of blooms of the motile forms. Although the cyst record is taxonomically very limited in its coverage of HAB species,

analysis of cysts has been used to recreate bloom patterns of dinoflagellates in the genus *Alexandrium* in Puget Sound, Washington State (Cox et al., 2008; Feifel et al., 2012). Warmer air temperatures and sea surface temperatures (SST) were significantly and positively correlated with cyst abundances from the late 1800s to 2005 (Feifel et al., 2012). Ancient DNA isolation from sediment cores, albeit a research field still in its infancy, offers considerable promise for more complete analysis of historical community structure (e.g., Klouch et al., 2016).

Even for long HAB time series that span multiple cycles of natural patterns of climate variability, the HAB response to the warm periods of the past may not be representative of future conditions. This is because the warm periods of the past are projected to be cooler than even the cool periods of the future (Overland and Wang, 2007). That is, climate change is expected to result in future ocean conditions that will be unlike anything experienced in the documented past, limiting our ability to look to the past to predict the future. Thus, events that today are considered "extreme" are likely at the lower threshold of what might be expected in the future, but nevertheless serve as important natural experiments to forecast what is to come.

1.1. Extreme events

In many cases, extreme weather events mimic future climate conditions and provide a "dress rehearsal" for understanding future frequency, intensity and geographic extent of HABs. Extreme weather events are naturally occurring, short-term, intense perturbations to the ocean-climate system. The short-term weather changes often may be similar to changes expected under climate change, providing a natural laboratory to study the effects of multiple stressors on HABs. Extreme weather will become more common with climate change. These extremes will have dramatic effects near the air-sea interface where pelagic phytoplankton reside. Heavy and extreme rain events have been associated with high SST (EASAC, 2013). This results from the elevated capacity of the atmosphere to hold water vapor as air temperature increases. This elevated atmospheric moisture will fuel storms on several spatial scales and will result in a greater likelihood of precipitation. Extra precipitation will cause a positive feedback loop, resulting in more intense precipitation events. On the other extreme, warming will enhance evaporation resulting in earlier snow melt and causing great summer drying. More frequent and longer heat waves with correspondingly fewer cold days and nights will be observed. The result will be greater extremes in precipitation and drought that will continue to increase with global warming (Trenberth, 2011).

The opportunity to study the response of HABs under extreme conditions provides a greater understanding of the multifactorial environmental effects that will combine to produce the most devastating events. According to the Intergovernmental Panel on Climate Change (IPCC, 2013), both gradual and more erratic changes in weather will be observed which, in turn, will be a major driver of changing HABs. In recent years, Europe has suffered a rising number of extreme weather events - from unprecedented heat waves and droughts to record-breaking floods, wind storms and freezes (Fig. 1). The number of hot days has increased 3-fold and the length of heat waves has doubled since 1880. Insurance industry data clearly show that the number of loss-related weather extremes has significantly increased on a global scale. There is increasing evidence that global warming drives some of these trends. These extreme events include damage due to heavy rainfall, drought, heat waves and fewer extremely cold days (EASAC, 2013).

Modelling studies are showing that extreme weather will also become more prevalent in other parts of the world. For example, the state of California in the U.S. will show increased hydroclimatic extremes including both floods and drought resulting from anthropogenic warming (Swain et al., 2018). These include "whiplash" events where the transitions from wet to dry and dry to wet periods become more rapid. Such rapid swings from wet to dry years will favor organisms that demonstrate the ability to adapt to environmental temperature extremes as demonstrated by the success of *Pseudo-nitzschia* along much of the U.S. west coast during the anomalously warm conditions of 2015. Precipitation also will vary markedly by year and season, especially in southern California. The contrast between long, dry summers and brief, wet winters is expected to become even more exacerbated in the 21st century (Swain et al., 2018).

Studying HAB responses to extreme events provides essential data on the success of HAB species relative to non-HAB species under ecologically stressful conditions. As with all living organisms, the responses of phytoplankton to environmental stressors are not necessarily gradual or linear. Many organisms have threshold responses and can be very sensitive to short periods of environmental extremes that deviate from "normal" conditions (Glynn, 1984; Stock et al., 2011). Separating the drivers of HAB events during extreme events is challenging but can be further resolved using culture studies with natural isolates from these events. Using isolates from these natural experiments allows us to study organisms' responses to shifting and often interactive environmental pressures under controlled conditions. Important questions to ask of these natural experiments are: What are the drivers within each of these examples that allowed the event to occur? What evidence do we have that each of these events are due to climate change? What is the socio-economic impact of each or how do we better quantify these impacts? And finally, how do these events inform our understanding of HABs in the future ocean?

Here we discuss three case studies of extreme HAB events that may be indicative of future climate change conditions. The first is a study of a diatom species of the genus *Pseudo-nitzschia* while the second and third examine pelagic flagellate blooms. These HAB events can be categorized as "extreme" because extensive time series allows them to be distinguished from "normal" blooms. In all three events described here, once the extreme HAB was differentiated from normal blooms, additional targeted monitoring was employed to improve the understanding of the climate drivers, the mechanisms that gave rise to the event and to document the societal response. These focused, opportunistic studies of nature's experiments allow for the identification of complex climate drivers of HABs, and to quantify the capacity of coastal communities to withstand them. The three case studies described here are not meant to be an exhaustive description of all that is known about climate change and pelagic HABs, but rather they highlight the value of studying extreme events in clarifying the multitude of factors that must be considered when analyzing the impacts of climatic change on HABs.

2. Case studies

2.1. Pseudo-nitzschia and domoic acid monitoring in the U.S. Pacific Northwest

Long term trends are emerging that link toxic *Pseudo-nitzschia* blooms and corresponding increases in DA concentrations in shellfish with warmer ocean temperatures. A correlation was observed between an increased growth rate potential of *P. australis* and the Pacific Decadal Oscillation (PDO) with a 1-month lag and a 3-month lag with the mean Ocean Niño Index (ONI; McCabe et al., 2016). Similarly, a 25-year record of razor clam DA showed a strong relationship with the PDO with zero lag and a 3-month lag with the ONI (McCabe et al., 2016). The lag period may be a requisite "pre-conditioning" of seawater necessary for the observed biological response. The positive relationship between *P.*

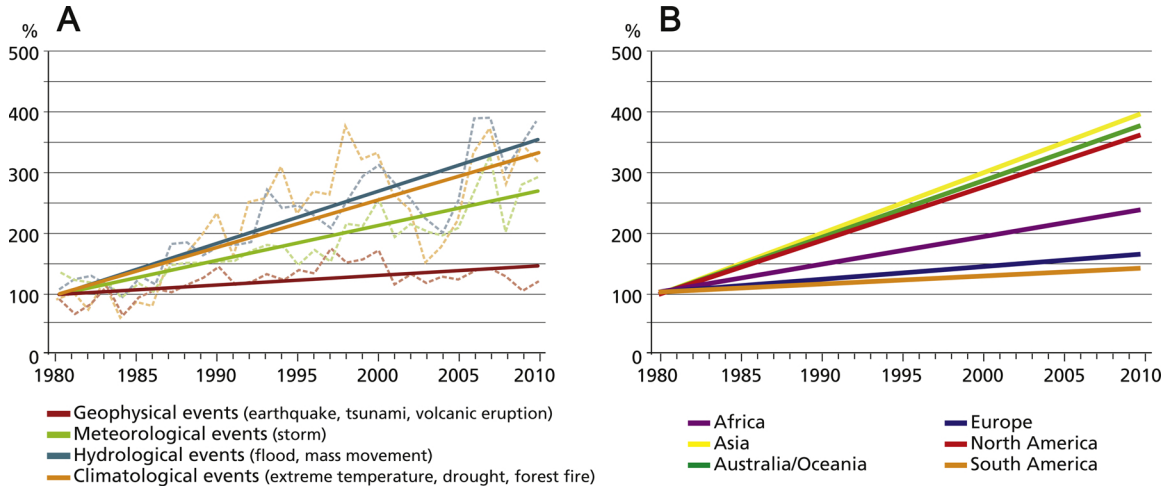

Fig. 1. Trends in numbers of extreme events worldwide, defined as those non-linear climate anomalies causing above average socio-economic losses. (A) Trends in types of different catastrophes worldwide, 1980–2002. Dotted lines connect annual average data; solid lines show linear trends; (B) Relative trends of loss-relevant natural extreme events in different parts of the world. For both panels, 1980 levels are set at 100%; data from Munich Re NatCatSERVICE); reprinted with permission (EASAC, 2013).

australis growth rate potential and warm anomalies, including the PDO, El Niño as well as the Pacific warm anomaly in 2015, illustrate the likelihood of more frequent DA contamination of shellfish during warmer years (McCabe et al., 2016; McKibben et al., 2017). This information linking damaging DA closures to warmer years currently is being used by coastal managers, thereby enabling greater preparedness in coastal communities.

In late Spring 2015, a massive, nearly simultaneous bloom of *Pseudo-nitzschia* occurred along the west coast of North America, spanning the California Current System (CCS) from central California to at least as far north as British Columbia. Harmful consequences resulting from the food web transfer of DA caused closures of Dungeness crab, rock crab, razor clam and other fisheries, as well as the mortality of numerous marine mammals and seabirds (McCabe et al., 2016; McKibben et al., 2017). Coastal communities suffered severe losses from fisheries closures - the commercial Dungeness crab fishery alone experienced a USD$97.5 million decrease in revenue in 2015 relative to 2014 due in part to the DA closures (NMFS, 2016).

A sequence of environmental changes occurred in response to a warm water anomaly ~3 °C above average SST to cause a "perfect storm" of shellfish closures and animal mortalities. This northeast Pacific marine heatwave, commonly known as the "Blob", began to develop in the Gulf of Alaska in late 2013 and continued to spread in 2014 and 2015 (Bond et al., 2015). The SST anomalies were caused by reduced heat exchange between the ocean and atmosphere, relatively poor advection of cool water in the upper ocean, and reduced storm-driven mixing (Bond et al., 2015). Nutrient renewal from vertical transport was restricted in winter of 2014-15 due to increased stratification (Peña et al., 2018). Climate model simulations combined with observations suggest that marine heatwaves in the North Pacific, like the Blob and its associated drought that was particularly notable in California, may intensify with climate change (Wang et al., 2014, 2015; Yoon et al., 2015; Di Lorenzo and Mantua, 2016).

During the 2014–16 northeast Pacific marine heatwave, low primary productivity was noted (Whitney, 2015) and anomalously low nutrient concentrations were observed off central Oregon (Du et al., 2016) and station P (Peña et al., 2018) in the northeast subarctic Pacific. Record numbers of marine mammals were observed close to shore in California, with decreased nutrient concentrations in the warm water anomaly contributing to cascading effects throughout the ecosystem. This warm water did not support living marine animals due to the depleted nutrients and collapse of the food web offshore, similar to nutrient depletion experienced during other warm (El Niño) events (Chavez et al., 2002). Specifically, a record number of Guadelupe fur seals, Northern fur seals, and California sea lion pups were rescued by the Marine Mammal Center in Sausalito, California in 2015. The sea lion pups were younger and thinner than typically seen, further evidence of the lack of food in the coastal seas (TMMC, 2015). The Marine Mammal Center stated "we cared for more than 200 patients at our hospital every single day for 3 solid months"; animals suffered from starvation, DA poisoning or both. The scarce prey that was available for mammals, such as sardines and anchovies, were highly contaminated with DA. All planktivorous fish, including Northern anchovy (*Engraulis mordax*), Pacific jack mackerel (*Trachurus symmetricus)*, Pacific sardine (*Sardinops sagax*), Pacific herring (*Clupea pallasii*), and eulachon (*Thaleichthys pacificus)* collected primarily in California coastal waters and analyzed for DA (n = 45) contained measurable DA with the highest concentration measured in anchovy viscera at an astounding 3239 ppm (Fig. 2). There was a general trend of decreasing toxicity with increasing latitude, consistent with the survey sampling northern latitudes late in the bloom when DA was declining.

By spring 2015, the warm anomaly moved toward the coast of North America. A research cruise off Newport, Oregon, in April 2015 showed that toxic *P. australis* cells were present within the warm water mass (W. Peterson, pers. comm.). A mooring off the Oregon coast showed that peak SSTs reached the coast in April 2015, followed immediately by the spring transition to upwelling (Du et al., 2016). A series of spring storms in May 2015 brought the toxic cells to the coast where they were fueled by macronutrients from upwelling, resulting in a coastal bloom that contaminated shellfish coastwide with DA at concentrations above the regulatory threshold beginning on 8 May 2015 (Fig. 3, vertical dotted line).

How did *P. australis* survive in these nutrient-deprived, warm waters, and then thrive to develop into a monospecific, highly toxic and devastating HAB under this sequence of changing conditions? Clearly *P. australis* can sustain itself under extreme environmental conditions, positioning itself to outcompete other phytoplankton and bloom to high densities when provided with adequate nutrients for exponential

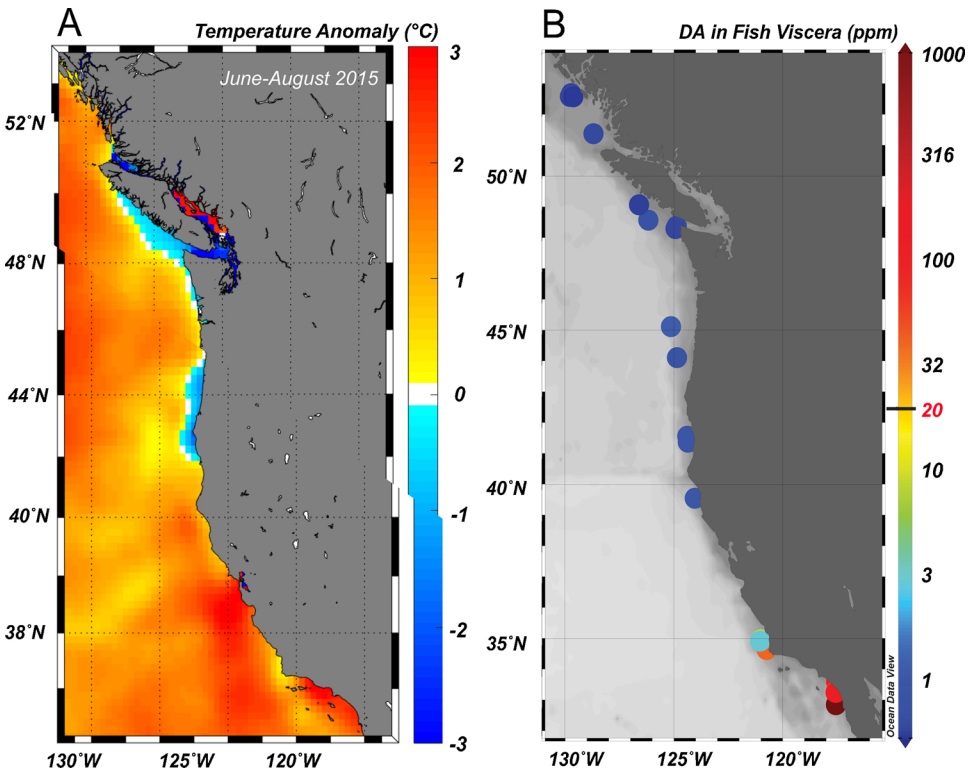

Fig. 2. Temperature anomaly and DA in fish viscera during a west coast cruise. (A) Anomalously warm surface water in the North Pacific Ocean as shown by mean sea surface temperature anomalies (°C) from the NCEP/NCAR Reanalysis for June-August 2015; (B) All fish viscera (northern anchovy, herring, Jack mackerel, sardine) collected from the 2015 west coast survey (transit from south to north; June - Sept 2015) were positive for DA with values ranging from 0.02 to 3238.6 ppm. The regulatory closure level of 20 ppm is shown in red on the right y-axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

growth. A suite of physiological characteristics may have permitted this particular species to respond in such a dramatic fashion in 2015. These include its ability to acquire strongly complexed iron, even when available at very low concentrations, using a high-affinity iron acquisition system that requires copper and the production of DA (Wells et al., 2015); in fact, another massive bloom of *Pseudo-nitzschia* was reported a decade earlier in the northern CCS under low Fe conditions, but when macronutrients were plentiful (Trainer et al., 2009; Trick et al., 2018). In addition, the high affinity of *P. australis* for nitrate and ammonium (Cochlan et al., 2008) would provide this species with a competitive advantage for acquiring nitrogen (N) under N-depleted conditions, but especially following upwelling during N-replete conditions where its maximal rate of nitrate uptake exceeds those of virtually all the other phytoplankton species commonly found in upwelling systems (Kudela et al., 2010). It is also possible that *P. australis* may share the short-term 'surge uptake' capability seen for smaller-celled species of *Pseudo-nitzschia* (Auro, 2007; Bill, 2011), where N-starved cells can rapidly respond to elevated N concentrations by acquiring nitrogen at uptake velocities that greatly exceed cellular growth requirements, but this has not yet been examined for *P. australis*. Although the details are not entirely clear, the ability of *P. australis* to survive marine heat waves, and the resultant conditions of warmer, nutrient depleted waters suggest that this toxic species will be a more frequent occupant of the future ocean.

While it is clear that the spring upwelling provided the needed macronutrients to support the growth *P. australis* to high densities throughout the CCS, these upwelled waters had subtle, but potentially very different impacts on the toxicity of the 2015 bloom, in particular during its initial development. In Monterey Bay (southern CCS), the upwelled waters initially eliminated anomalously warm surface waters associated with the Blob. Thus, although were no direct impacts on *P. australis* growth rate from increased water temperature, the unusual chemical composition of these upwelled waters, specifically the anomalously low SiO_4: NO_3 ratios, led to silicate exhaustion in surface waters, whereas nitrate remained available throughout the bloom development (Ryan et al., 2017). Given that cellular DA quota (particulate DA per cell) depends on the balance between rates of DA synthesis and rates of cell division, silicate limitation may have been the proximate cause of elevated DA toxicity in Monterey Bay by decreasing cell division rates without any increase in per-cell DA production rates. Here the plentiful nitrate supported exceedingly high abundances of *Pseudo-nitzschia* which were overwhelmingly *P. australis* (Bowers et al., 2018). Domoic acid quotas reached high levels within these dense populations (Ryan et al., 2017) due to the eventual exhaustion of silicate, while nitrate remained available for continued DA biosynthesis rates as reported in culture studies following silicate (or phosphate) depletion for other *Pseudo-nitzschia* species (cf. reviews by Bates, 1998; Lelong et al., 2012; Trainer et al., 2012). In contrast, further north in the CCS off Oregon, the cool nutrient-rich upwelled waters did not initially eliminate the anomalously warm waters at the coastal margin. The upwelled water mixed with the overlying and adjacent warm waters of the Blob and *P. australis* bloomed not only because of the supply of upwelled nutrients, but also due to the direct effect of temperature on cellular growth, seen in the thermal growth response curves for three strains of *P. australis* isolated from this bloom (McCabe et al., 2016). Here, unlike Monterey Bay, ambient silicate concentrations rarely were lower than nitrate (Du et al., 2016), and warmer temperature was likely the primary physiological factor in the development of the toxic diatom bloom in the northern CCS. Even further south (e.g., the Southern California Bight), there were no toxic blooms in 2015, presumably due to the supraoptimal temperatures (Smith et al., 2018). Here, substantial DA concentrations have never been seen at water temperatures > 19 °C (Smith et al., 2018).

Examining the response of *Pseudo-nitzschia* across the full domain of the CCS also reinforces the difficulty of broadly generalizing from limited studies. *P. australis* generally does well in warm (but not hot)

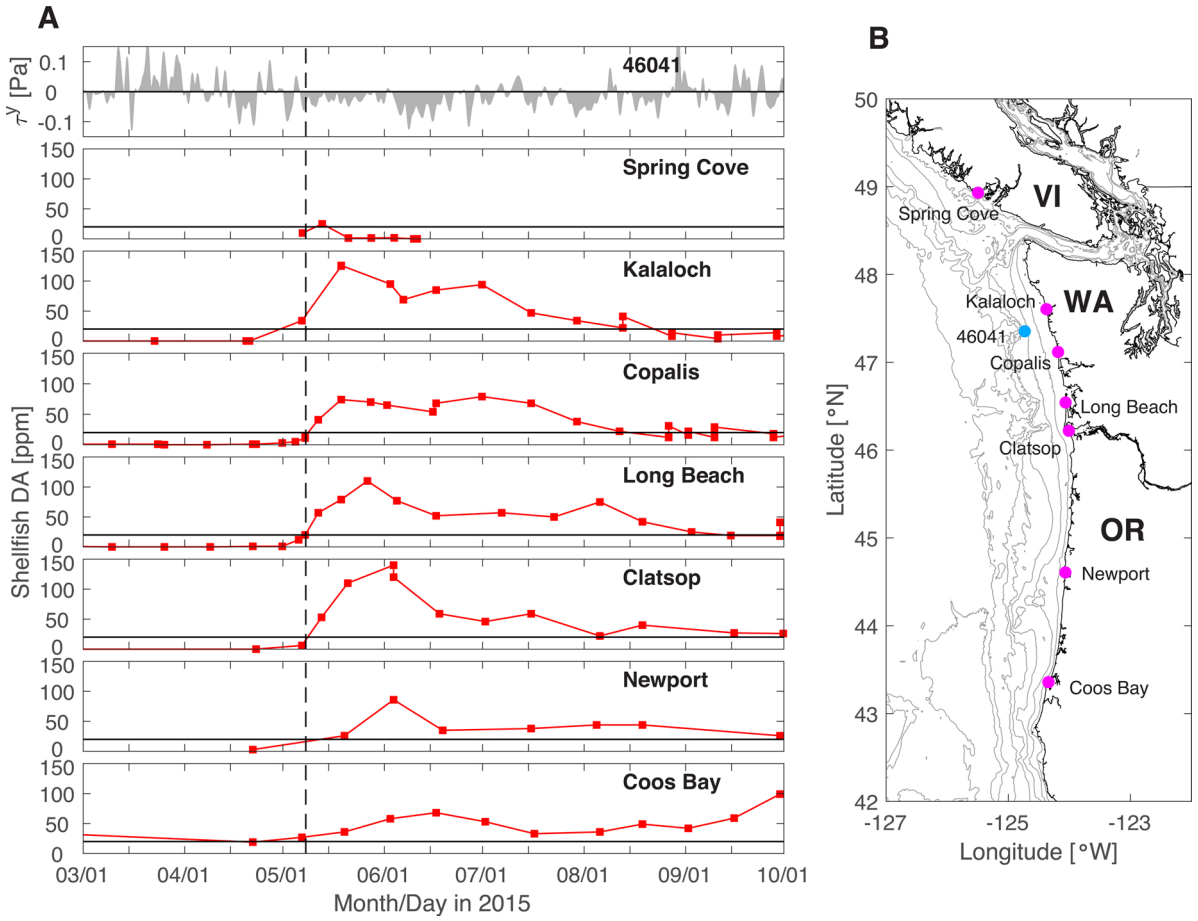

Fig. 3. Shellfish harvesting beaches and DA concentrations in razor clams. (A) Razor clam DA at beach sites in Oregon (OR), Washington (WA) and British Columbia (Vancouver Island, VI) with north-south wind stress. Dotted line shows that on May 8, shellfish beaches showed a simultaneous increase in DA concentrations. Winds above the zero line indicate storms or northward wind stress; the 3 storms in late April and early May transported *Pseudo-nitzschia* cells toward the coast; (B) Map of beaches where razor clams or mussels (Spring Cove only) were monitored for DA (pink circles); data shown in panel A. Wind data were accessed from the National Data Buoy Center mooring at Cape Elizabeth, WA (46041; blue circle). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

water with weak to moderate upwelling (Kudela et al., 2004). Restructuring of the East Pacific provided a "window of opportunity" for *Pseudo-nitzschia* dominance in place of the usual springtime centric diatoms that include *Chaetoceros* spp., *Skeletonema costatum* and others (e.g., Venrick, 1998). Conditions have been shifting for the last several years towards warmer, nutrient-depleted water, amplifying the unusual conditions in 2015 (Fig. 4). However, even though there is strong evidence for a thermal limit of > 19 °C for production and accumulation of DA from extant natural populations (Smith et al., 2018 and Fig. 5), optimal growth rates were reported at 23 °C for one strain of *P. australis* isolated from southern California (Zhu et al., 2017). Here cellular DA concentrations were not even detected until this temperature was reached, and then DA increased exponentially with rising temperature above 23–30 °C, even as growth rates were crashing,

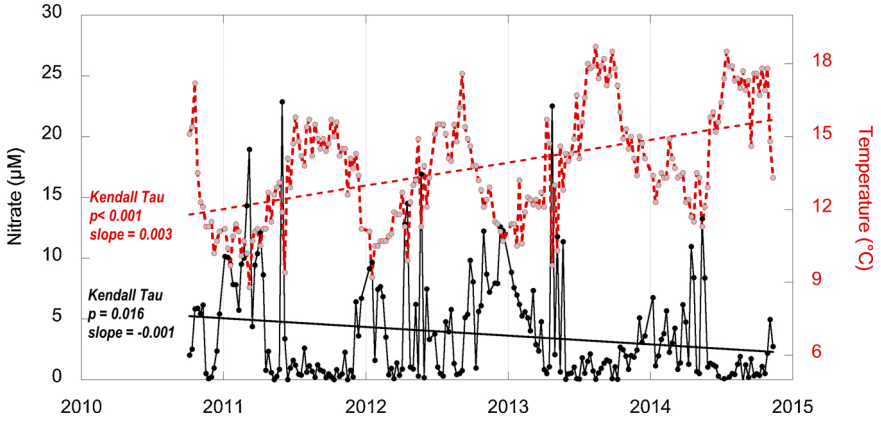

Fig. 4. Data collected from the Santa Cruz Municipal Wharf (Monterey Bay, CA) weekly from 2012 to 2016 show significant trends of increasing sea surface temperature and decreasing nitrate over multiple years.

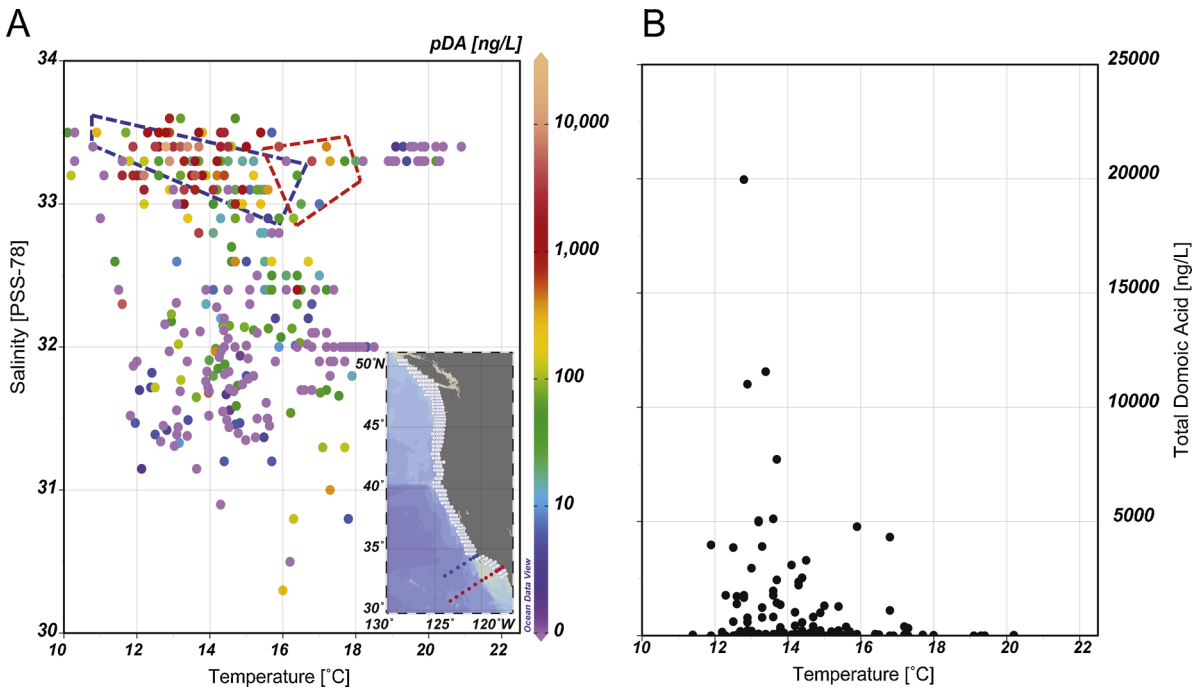

Fig. 5. In southern California, it was too hot to support *Pseudo-nitzschia* growth and DA production. (A) The temperature-salinity plot shows particulate DA (pDA) concentrations from a 2015 west-coast survey (McCabe et al., 2016). The highest DA (and presumably *P. australis*) was associated with cool(er), salty water, indicative of Blob water mixed with local upwelling. The blue dashed polygon shows the T-S space (0–10 m) for CalCOFI Line 80 (off Santa Barbara, inset, blue transect) immediately after the Spring Transition, while the red polygon shows the T-S space for Line 90 (off southern California, inset, red transect). As the season progressed those regions warmed, reducing the realized habitat for toxic *P. australis* in the south, while expanding it northward into the Pacific Northwest; (B) The survey data for total DA versus temperature. Consistent with Smith et al. (2018), no substantial DA was detected above 18°C. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

resulting in cellular DA quotas increasing by 70-fold in this upper temperature range.

Pseudo-nitzschia species matter as do their specific responses to changing environmental conditions. During the 2015 event, *P. australis* emerged from a background of multiple *Pseudo-nitzschia* species, and dominated along almost the entire U.S. west coast, whereas during other years, less toxic species such as *P. delicatissima* can dominate, resulting in large blooms but with lower toxicity (Smith et al., 2018; Bowers et al., 2018). Under future conditions, we may see selection for species or strains that have not emerged in the historical record, and are therefore poorly characterized. This could be exacerbated when considering multiple stressors such as warming, increased hypoxia, and ocean acidification - stressors that are all expected to intensify in the CCS as a result of anthropogenic change (cf. reviews by Capone and Hutchins, 2013; Raven et al., 2019 this issue). Recently, the interactive effects of increased temperature and pCO_2 were examined with N-limited continuous cultures of natural assemblages from southern California containing *P. multiseries* and *P. hasleana.* Although temperature individually appeared to have the strongest influence on cellular DA quotas, there were conflicting pDA responses to pCO_2 depending on the N substrate used for growth and the temperature tested, and the authors concluded that there was no consistent toxic response to pCO_2 nor to the interaction of temperature and pCO_2 (Tatters et al., 2018)

It is clear from this case study that warming was a significant factor in the unprecedented west coast-wide *Pseudo-nitzschia* bloom, but the bloom was not necessarily the result of a linear physiological response to increased temperature. The northeast Pacific marine heatwave allowed *P. australis* to expand or shift northward but exceeded the apparent temperature threshold for DA production in the southern regions of the CCS (Fig. 5) where toxic blooms did not develop in 2015, and where substantial DA concentrations have never been observed at temperatures > 19 °C (Smith et al., 2018). The temperature signal is almost certainly a proxy for other co-varying environmental factors such as nutrient availability (Ryan et al., 2017), and there appears to be considerable species and strain variability that could favor both more or less toxic organisms under future climate conditions.

The socioeconomic and cultural damage to communities as a result of the 2015 HAB event were described in a recent study of two U.S. west coast fishing communities that are both highly dependent on the commercial Dungeness crab fishery for income and have a substantial recreational razor clam fishery (Ritzman et al., 2018). In person, semi-structured interviews assessed the sensitivity and adaptive capacity of these communities to the HAB event. Documented economic hardship spanned the communities, and included processors and fish markets, restaurants, hotels, retail and tourism sectors. Some interviewees feared that a repeat event would result in a cultural shift away from both recreational and commercial fishing. Understanding the social, cultural and economic hardships faced by coastal communities is an essential part of the scientific storytelling of HAB events. Community members emphasized the importance of preparing for the future which includes fully describing and communicating impacts to legislative authorities who can sponsor mitigative strategies to reduce the shock of extreme HABs.

2.2. *Alexandrium dinoflagellate and toxin monitoring in Tasmania, southeast Australia*

Starting in 1985, the Tasmanian shellfish industry had become used to closures and public warnings of paralytic shellfish poisoning (PSP) risks inflicted by *Gymnodinium catenatum* dinoflagellate blooms in the Huon River and d'Entrecasteaux Channel near the capital city of Hobart, Tasmania, Australia (Hallegraeff et al., 1995). After experiencing recurrent shellfish farm closures in this region for a decade, this problem was largely solved by declaring the affected estuaries unfit for shellfish aquaculture. Early HAB surveys of other Tasmanian locations, including the east coast, had revealed low concentrations of

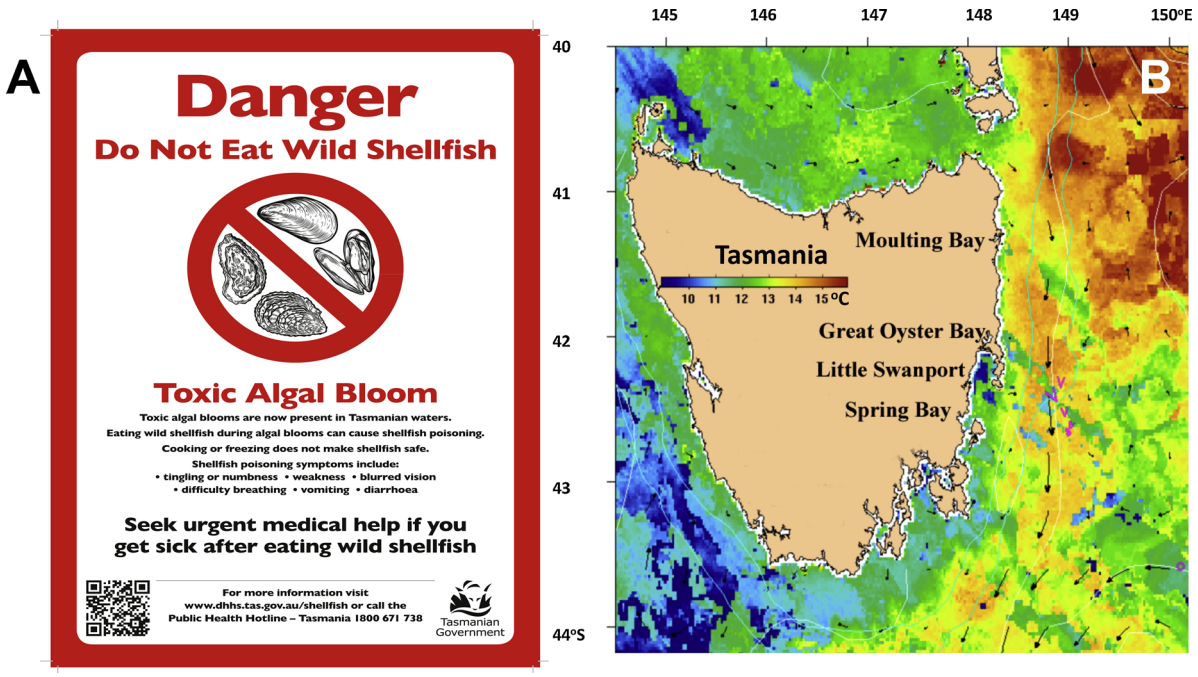

Fig. 6. Signage and SST during the anomalous PST event in eastern Tasmania. (A) The first toxic algal bloom warning signs posted along the entire east coast of Tasmania to prevent further human poisonings and protect tourism. Courtesy: https://www.dhhs.tas.gov.au/_data/assets/pdf_file/0005/264227/Marine_Biotoxin_Warning_6pp_DL.PDF; (B) Map of Tasmania, south of the mainland of Australia, showing sea surface temperatures on 27 September 2015 during peak PST, with the East Australian Current (in red) interacting with the continental shelf. The locations of the main affected shellfish farm areas Moulting Bay, Great Oyster Bay, Little Swanport and Spring Bay are indicated. Source: oceancurrent.imos.org.au. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Alexandrium tamarense group 5 (non-toxic; now designated *A. australiense*) and only once group 4 (weakly toxic; now designated *A. pacificum*) and the area was therefore classified as a low biotoxin risk, subject to limited plankton and biotoxin monitoring. Unexpectedly in October 2012, a shipment of cultured blue mussels was tested by Japanese import authorities and shown to be contaminated with 10 mg/kg paralytic shellfish toxin (PST; 0.8 mg/kg is the regulatory closure level). This led to a global product recall and loss to the local economy of AUD$23 M. The causative organism proved to be highly toxic blooms of *A. tamarense* group 1 (now designated as *A. catenella*) not detected previously in any Australian or New Zealand waters (Hallegraeff et al., 2017). Following low toxicity during 2013 and 2014, more severe bloom events occurred during 2015, 2016 and 2017 (up to 300,000 *Alexandrium* cells L^{-1}; up 150 mg kg^{-1} PST in mussels, 22 mg kg^{-1} PST in oysters; 14 mg kg^{-1} PST in rock lobster viscera; 1.3 mg kg^{-1} PST in abalone viscera), also causing 4 people to be hospitalized after consumption of wild shellfish (human poisoning syndromes reported by Edwards et al., 2018). Both culture experiments but notably field estimates suggested a high cellular toxin content up to 100–500 pg STX eq $cell^{-1}$, explaining why even very low *Alexandrium* concentrations (50–100 cells L^{-1}) occasionally can cause shellfish toxicity.

To protect tourism and human health, the east coast of Tasmania has posted permanent public HAB warnings since 2017 (Fig. 6), which is a first for Australia. Until these bloom events began in 2012, the island state of Tasmania had very limited biotoxin analytical capabilities, with samples routinely shipped and tested in Sydney, thereby leaving the Tasmanian seafood industry in limbo for 7–10 d awaiting test results. To assist the industry, a major effort was made to introduce and validate rapid (20 min) immunological test kits, allowing for shellfish farmers to perform PST tests at their farms before making decisions on harvesting (Dorantes-Aranda et al., 2017). Extensive training courses were organised to ultimately provide individual farmers with certificates of competence. Negative test results were accepted by regulators, while positive test results required confirmation by analytical laboratories. Starting in 2018, Tasmania invested in a dedicated biotoxin laboratory.

Preliminary investigations of meteorological and oceanographic conditions from 2012-17 indicate that the annually recurrent winter-spring *Alexandrium catenella* blooms (June-October) occur within a narrow temperature window (10–15 °C) under two distinct sets of conditions: (1) following high rainfall and land run-off; and (2) following periods of anomalously low air temperatures and associated cooling of shallow coastal waters. The common driver of blooms appears to be stratification in coastal waters via salinity and temperature gradients. The ocean environment east of Tasmania is a well-documented climate change hotspot (Fig. 6), characterized by a stronger East Australian Current (EAC) and rapidly increasing ocean temperatures (2.3 °C warmer since the 1940s) and associated changes in fish, plankton and kelp communities (Johnson et al., 2011). Thermal stratification usually occurs on the continental shelf over late spring (November) but since 2009 the strengthening EAC has been accompanied by earlier development of stratified conditions. While there is no evidence that blooms originate offshore, the offshore environment may play a role in moderating coastal water conditions. At times, *Alexandrium* blooms off eastern Tasmania may also be influenced by climate driven changes associated with seasonal rainfall. Bloom events in 2012, 2013 and 2016 followed high rainfall, resulting in enhanced coastal stratification. Coastal stratification also intensified during the 2015 and 2017 bloom periods, but through a different mechanism involving the subsurface outflow of anomalous cold water from Great Oyster Bay and Spring Bay (Condie et al., 2019). Decreased silicate concentrations associated with a strengthening EAC would further favor dinoflagellates and select against competing diatom blooms (Thompson et al., 2009). Climate forecasts for the Tasmanian region predict gradually decreasing total rainfall, but an increase in the frequency of heavy downpours (Grose et al., 2010). With ever increasing water temperatures also in winter months projected for the decades to come, this could reduce the seasonal bloom window for the colder-water *A. catenella*.

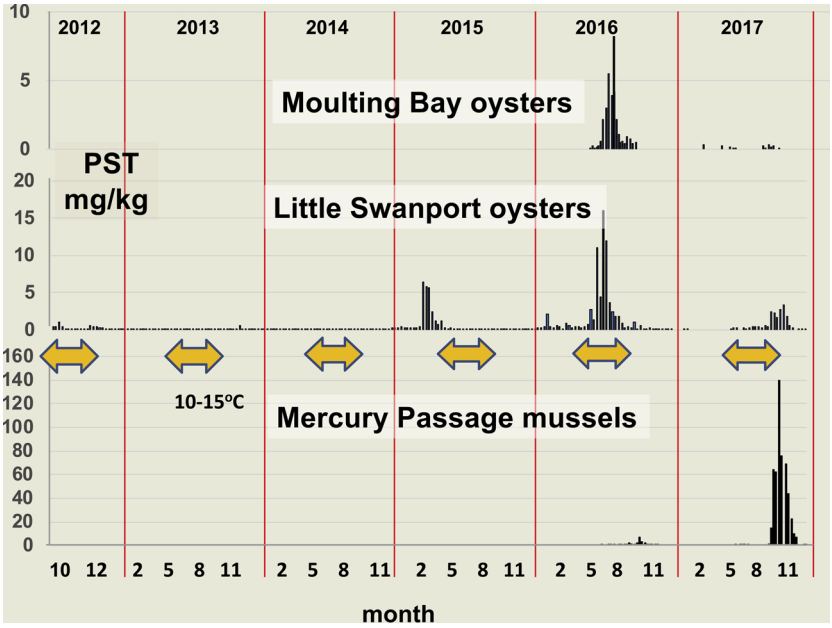

Fig. 7. Shellfish toxicity (mg STX eq. kg^{-1}) from 2012 to 2017 in Moulting Bay and Little Swanport oysters and Spring Bay mussels. Orange arrows indicate the seasonal 10–15 °C temperature window. The 2016 bloom was preceded by a major rainfall event while anomalously cold water in Great Oyster Bay (Little Swanport) may explain the 2015 bloom. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Our current understanding of these novel *Alexandrium* blooms is that they are not a simple response to increasing water temperatures, since they occur during the cold winter-spring months (Fig. 7). Genetic evidence (John et al., 2018) indicates that the Tasmanian *A. catenella* group 1 populations exhibit a unique microsatellite signature and therefore do not represent a ballast water introduction nor range expansion (Sydney coastal waters exclusively host *A. pacificum*). Preliminary sediment DNA results (Shaw et al., 2019) suggest that *A. catenella* did exist in Tasmanian waters as early as 1987 but simply had been overlooked. *Alexandrium* cyst surveys during August 2016 along the entire east coast of Tasmania found consistently low abundances of cysts (0.1–3 cysts per gram of sediment wet weight; Hallegraeff et al., 2017). This also suggests that these blooms are recent events. Palaeogenomic research is in progress using ancient DNA methods on dated sediment depth cores (11,000 years old) from the area to document historic shifts in *A. tamarense* ribotypes 1, 4 and 5, in support of this recent blooming phenomenon. No historic records of shellfish poisoning are known from the Tasmanian region by Aboriginal tribes for whom shellfish comprised a significant part of their diet (Jones, 1978). Our working hypothesis is that these dinoflagellates represent a previously cryptic genotype newly stimulated by climate-driven increased water column stratification during winter and early spring. The major lessons learned from this extreme Tasmanian HAB event are that prediction of the impact of global climate change on marine HABs is fraught with difficulties, and that the greatest problems for human society will be caused by range expansions or the increase of algal biotoxin problems in poorly monitored areas.

2.3. Record HAB events in Chilean fjords in 2016 by Pseudo-chattonella cf. verruculosa and Alexandrium catenella

The Chilean inland marine waters (Fig. 8A) are a unique Southern Hemisphere ecosystem that supports a variety of economic activities, especially fishing and aquaculture, providing employment and economic services for thousands of people. To date, most of the shellfish and salmon farming activity is within the Los Lagos region (41–44 °S) with an increasing development further south. Salmon farming commenced in the Chilean fjords in 1982 and currently is valued at USD $4.3 billion per year (León-Muñoz et al., 2018). Over the past decades the salmon industry has faced a number of setbacks from disease outbreaks and fish-killing algal blooms (Little et al., 2015). Local impacts of algal blooms on the salmon industry date back to 1983 (Lembeye and Campodónico, 1984). In 1988, a bloom (100,000 cells ml^{-1}) of the raphidophyte *Heterosigma akashiwo* killed 5000 tons of salmon valued at USD$11 M (Clement and Lembeye, 1993). This extreme biological event in 1988 triggered the start of an extensive plankton monitoring program by the Chilean Salmon Association which was followed by other private and governmental organizations (i.e., Plancton Andino SpA and the Institute for Fisheries Development – IFOP). In summer of 2000, the same species bloomed again and caused the mortality of 40% of the farmed salmon in the Reñihue fjord. In that event, as few as 40 cells ml^{-1} of *H. akashiwo* coupled with a high concentration of *Leptocylindrus danicus* produced a very large salmon kill at only one salmon farm, pointing to the high potential ichthyotoxicity of this flagellate in a synergistic action with the diatom. However, the most damaging and extreme event in the history of the salmon industry involved two other ichthyotoxic microalgae; the dictyochophyte, *Pseudochattonella,* (referred to until 2011 as the raphidophyte *Chattonella*) and the dinoflagellate, *Alexandrium catenella*.

During the warm January of 2004, *Pseudochattonella* cf. *verruculosa* (8 cells/ml) was recorded for the first time together with an outbreak of *Vibrio parahaemolyticus* in Los Lagos region, causing the mortality of 2–5% of the total farmed salmon in the Reloncavi Sound (Mardones et al., 2012). This species was regularly detected in 2004, 2009, 2011 and 2016 in the same area. During the first recorded bloom, *P.* cf. *verruculosa* cell density reached a maximum of 22 cells ml^{-1} at a water temperature of 15 °C, whereas in later events peak abundances reached > 400 cells ml^{-1} at water temperatures of 18.5 °C (Mardones et al., 2012). Even higher concentrations recently were detected in 2016 in the northern Patagonian fjords, considered the most significant event to date in that area. Altogether, these spatial-temporal records show an increase in bloom intensity and a clear expansion of *Pseudochattonella* cf. *verruculosa* towards the southern areas (Fig. 8B).

In contrast, *Alexandrium catenella* blooms have shown an expansion towards the north of Chile in recent years (Fig. 8C). This dinoflagellate was first reported in Chile in 1972 in the Bell Bay-Magallanes Region (~54 °S) (Guzman and Campódonico, 1975). Subsequently, *A. catenella* was detected outside the mouth of the Aysén fjord, near Churrecue Island in May 1992 (Muñoz et al., 1992). It is believed that this was the first sign of a gradual northward dispersion of the species. Later in 1998, cells of this toxic dinoflagellate were observed in net tow samples collected near the Quellón area, Chiloé Archipelago (Lembeye et al.,

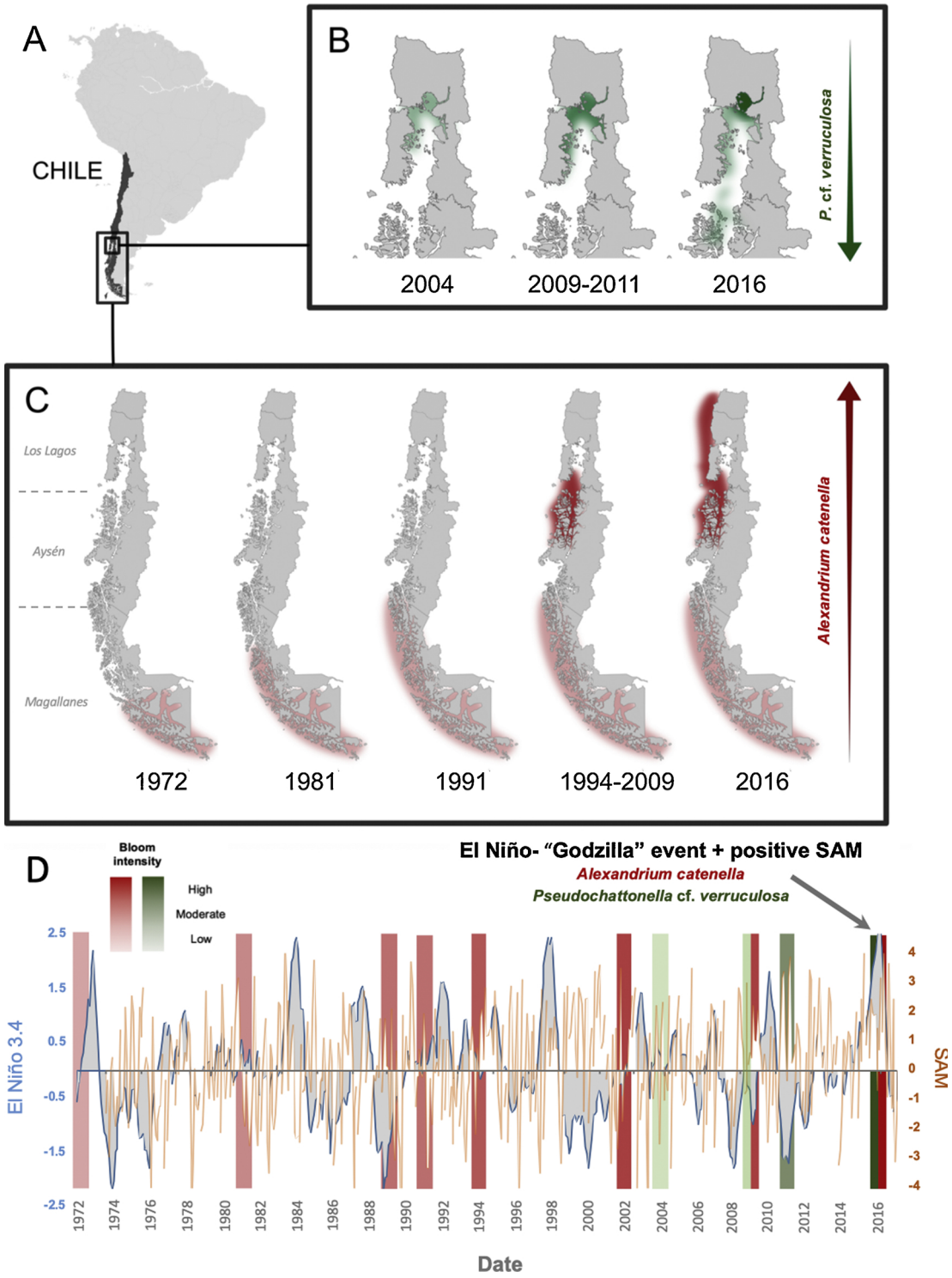

Fig. 8. Location of HAB species and their relationship to climate indices during the 2016 Godzilla HAB event in comprison to previous years. (A) Patagonian fjords in the South of Chile; (B) Southern expansion of *Pseudochattonella* sp. (Mardones et al., 2012; Clement et al., 2016); and (C) northern expansion of *Alexandrium catenella* (Mardones and Clement, 2016) blooms in Chilean fjords, and (D) blooms that have expanded the spatial distribution of *Pseudochattonella* sp. and *A. catenella* in the Chilean fjords associated with the El Niño 3.4 index (blue line) and the Marshall Southern Annular Mode (SAM) index (orange line). The intensity of the *A. catenella* and *P. verruculosa* blooms is indicated by the intensity of the red and green vertical bars, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

1998) at least 350 km north from Aysén fjord. However, the most important outbreak with a maximum of 778 cells ml^{-1} was in summer of 2002 in the southern Chiloé Archipelago (43 °S) (Clement et al., 2002).

The first farmed trout kill due to *A. catenella* occurred in Churrecue Island, near Aysen fjord, in March 1996 with a maximum abundance of 1184 cells ml^{-1}, forming patches of reddish water discoloration. During the summer of 2005 and 2006, blooms of *Alexandrium catenella* (by then a well-known PST producer) were detected in the northern fjords of the Aysén region. The bloom caused 7 human intoxications and one fatality. Unusual behavior of farmed salmon, coincident with

high *A. catenella* abundance in surface waters of fish farms (> 356 cells ml^{-1}) preceded fish gill damage and an extensive fish kill (Fuentes et al., 2006). Later in 2009, a massive bloom (ca. 5000 cells ml^{-1}) that covered a wide geographical area from 46°to 43°45′S, was associated with 20 human shellfish poisonings, 2 fatalities and more than USD $10 M in losses to the Chilean salmon industry (Mardones et al., 2010).

During the austral summer (February-March) of 2016, both *P.* cf. *verruculosa* and *A. catenella* produced the most catastrophic event in the history of Chilean aquaculture, with record socio-economic impacts. Together, these two massive blooms were colloquially known as the "Godzilla-Red tide event" and occurred in two stages. The first HAB event in February was associated with a bloom of *Pseudochattonella* cf. *verruculosa* (max. ~20,000 cells ml^{-1}) in the Reloncaví Sound and close to Chiloé Archipelago, producing the largest fish farm mortality event ever recorded in the world. Losses for the salmon industry in this occasion were calculated as 100,000 metric tons of Atlantic and Coho salmon and trout, equivalent to an export loss of USD$800 million (15% of Chile's yearly production; Clement et al., 2016). All evidence points to exceptional ocean and inshore water conditions produced by a strong El Niño event and the positive phase of the Southern Annular Mode (SAM; Fig. 8D) that altered the atmospheric circulation in southern South America and the adjacent southeastern Pacific Ocean (León-Muñoz et al., 2018). The positive phase of the SAM is an indicator of modern-day decreases in both precipitation and stream flow (Jones et al., 2016) in a region of traditionally high precipitation associated with a prevailing westerly flow off the Pacific Ocean with orographic lift of the southern Andes (Viale and Garreaud, 2015). Thus, SAM is a sign of anthropogenic climate change (Gillett et al., 2013; Gillett and Thompson, 2003; Arblaster and Meehl, 2006) that mediates changes in circulation and precipitation (Rebolledo et al., 2014). As El Niño conditions usually favor negative phases of the SAM (L'Heureux and Thompson, 2006; Ding et al., 2012), the fact that the SAM was at its highest positive phase during the summer of 2016 suggests that climate change had a strong enough influence to overcome the El Niño forcing (Wang and Cai, 2013), resulting in positive phases of both indices (Fig. 8D). This led to a strong drought with record low rainfall, reduced fresh water discharge, increased water temperature and stratification. The resultant increase in SST (> 15 °C) and reduced freshwater input allowed the advection of more saline (~33-34 salinity) and nutrient-rich offshore waters into the fjords, resulting in an active HAB in coastal southern Chile (León-Muñoz et al., 2018).

The second HAB event occurred in late March and most of April 2016. A major *A. catenella* event pushed further northward than ever before on the oceanic coast of Chile. The occurrences of PSP on the ocean coast of Chiloé Island and northern Los Lagos region were unprecedented and affected 200 shellfish farms (~15% reduction in harvest compared to 2015) and 600 km of benthic artisanal fisheries due to 4 mo. of closure. The loss of income on coastal communities ignited massively disruptive social protests that lasted three weeks. These protests were also encouraged by the belief that the *A. catenella* bloom was intensified by offshore dumping of farmed salmon that died in the previous *Pseudochattonella* bloom. Scientific studies from universities and the government pointed out that the *A. catenella* bloom event was caused by the exceptional El Niño oceanic conditions of early 2016 (Buschmann et al., 2016). This study, based on remote sensing and field collections, concluded that the offshore bloom originated from a seed population transported by northward winds from the southern Aysén region and fueled by upwelled nutrients and high-water temperature. The hypothesized effect of the dumped dead fish as the trigger of the massive 2016 HABs was discarded by modeling the distance the fish were dumped offshore, the water depth and the prevailing currents that transported the nutrients released by the dead salmon toward the west and north, and not towards Chiloé Island (the most socio-ecologically affected area).

It remains unclear whether PST events in southern Chile will continue to expand northward and/or *Pseudochattonella* blooms will intensify. Future climate conditions will likely affect bloom dynamics of these two HAB species. *Alexandrium* resting cysts that were deposited at the end of blooms can serve as initiation sites for future outbreaks and possibly continued northward expansion (Mardones et al., 2016). Recent studies on the physiological response of the Chilean *Pseudochattonella* showed that increasing salinity stimulates in vitro cell growth (Mardones et al., 2019). These observations point to the important role of exceptional climate anomalies (i.e. as observed in 2016) in modulating future bloom dynamics of *A. catenella* and *Pseudochattonella* in the inner Chilean fjords.

3. Summary and conclusions

Extreme events allow scientists to more completely define and test models that describe the important drivers of blooms. However, there must be flexibility to mobilize rapidly to study extreme events, otherwise the opportunity to test hypotheses formed from laboratory experiments will be missed. These natural experiments, some of which are outliers of the associations derived from time series analyses, provide examples of how systems may respond to multiple stressors in the future. The rapid response to these events should include a human component that describes the socioeconomic and cultural impacts of extreme HAB events on communities and examine the governance structure. Clear investigative strategies and goals of such socioeconomic and cultural studies are important to identify policies that will allow communities to implement mitigative strategies to help them cope with future blooms.

In terms of scientific research, what went well during the responses to these extreme HAB events? For each of the events, time series of shellfish toxin content and phytoplankton abundance demonstrated that they fell outside range of historical HABs described for the region. For the extreme *Pseudo-nitzschia* event in the northeastern Pacific Ocean, participation on research cruises enabled mapping of the HAB distribution, species abundance and toxin concentrations during the bloom (McCabe et al., 2016; Figs. 2 and 5). Laboratory experiments on temperature regulation of cellular growth rates and cellular toxin were conducted with cell isolates from the bloom. Deployment of advanced, automated sampling equipment, such as the environmental sample processor (ESP) enabled mapping of the distribution of thin layers. Dedicated, routine collection of nutrient samples demonstrated the potential role of macronutrients in promoting specific blooms. An extensive social science study documented the response of coastal communities during the bloom and mapped the strategies for their resilience during future blooms. In Tasmania, the significant economic impacts of 7 years of recurrent seasonal PSP closures of the local mussel, oyster and lobster industries mobilized industry funded efforts to introduce and validate rapid immunological PST test kits and conduct industry training courses in their use in order to provide individual farmers and fishermen with the tools to make harvesting decisions. As a bonus, screening out negative test results meant huge cost-savings for industry in terms of analytical costs because in future only positive ELISA test results will require LC–MS confirmation by analytical laboratories. Furthermore, the local government now invested in setting up a dedicated analytical biotoxin laboratory in the State to secure seafood safety.

The Chilean salmon and shellfish industries clearly were not prepared for the extreme 2016 "Godzilla" bloom event. The mitigation strategies attempted at salmon farms during the *Pseudochattonella* bloom were not successful. The depth distribution of the harmful alga was not closely tracked resulting in the use of airlift-upwelling systems to pump water that may have contained dense *Pseudochattonella* "thin layers". In order to prepare for future events, the salmon industry is evaluating other mitigation methods, such as removal of blooms through clay dispersal and flocculation. In terms of shellfish monitoring, despite the large and extensive *A. catenella* bloom in 2016, no humans were poisoned. The Chilean Ministry of Economy and other

cooperating government agencies prepared a broad strategic plan that includes HAB monitoring and fisheries diversification in Los Lagos region. This last action should help minimize the economic impacts on the shellfish industry due to future PSP closures. The Chilean National Fisheries and Aquaculture Service (SERNAPESCA) issued several new aquaculture directives that include a moratorium on further aquaculture development in the southern fjords. This fact is of high relevance since, in the near future, the salmon industry had plans to increase Chilean salmon production, with an expansion in the southernmost and pristine Magallanes region. Furthermore, SERNAPESCA enacted a strict regulation requiring the industry to transport and process dead salmon in a timely manner. In terms of monitoring, recording of nutrients began in 2017 and the salmon industry has added more sampling sites for phytoplankton analysis. However, data sharing among the different entities that perform HAB monitoring currently is restricted and the identification of the fragile fish-killing flagellates is still extremely difficult by traditional microscope methods. Scientific collaboration and training initiatives by international and national HAB experts is increasing in Chile. Among the promising projects, the Japan International Cooperation Agency (JICA), in collaboration with CREAN-IFOP and Chilean universities, aims to predict HABs in the Chilean fjords through the analysis of triggering holobiome constituents.

What could be improved to more fully understand extreme events? Rapid initiatives and effective collaboration among scientists as well as appropriate mechanisms for emergency funding during such extreme events are of key importance in developing a mechanistic understanding of HAB development, and the inherent variability between toxic blooms of dinoflagellates and diatoms. There are apparently heat-tolerant *Pseudo-nitzschia* in the southern part of the CCS, and *A. catenella* was present but unidentified in Australia. This suggests that, as is stated in the introduction, the emergence of cryptic species and strains may play an increasing role in the successful competition of bloom species. Culture experiments with cell isolates from wide geographic study areas may help with identification and characterization of these cryptic cells. Ideally shipboard responses would have included the capability of performing deckboard experiments of natural assemblages to examine the role of macronutrients, trace metals and other environmental factors that regulated the blooms. Mesocosm or continuous culture studies would have clarified the responses of cells within the warm water anomalies to added pulses of macronutrients or trace metals in an attempt to replicate the bloom that occurred near shore. The social unrest caused by the extreme HAB events and displeasure expressed by communities in response to management actions highlights the need for better collaboration between social and natural scientists to inform policy and governance. Governments, including their associated environmental and health agencies, must understand that studying these extreme events provides a window into the future; and react by providing the support necessary to fully investigate them. Scientists must be poised to respond to future extreme HAB events while continuing persistent, dedicated monitoring at key sentinel sites around the world.

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References

Arblaster, J.M., Meehl, G.A., 2006. Contributions of external forcings to southern annular mode trends. J. Clim. 19, 2896–2905.

Auro, M.E., 2007. Nitrogen Dynamics and Toxicity of the Pennate Diatom *Pseudo-nitzschia cuspidata*: A field and Laboratory Based Study. MS Thesis. San Francisco State University, San Francisco 91 pp.

Bates, S.S., 1998. Ecophysiology and metabolism of ASP toxin production. In: Anderson, D.M., Cembella, A.D., Hallegraeff, G.M. (Eds.), The Physiological Ecology of Harmful Algal Blooms. Springer–Verlag, Heidelberg, Germany, pp. 405–426.

Batten, S.D., Walne, A.W., Edwards, M., Groom, S.B., 2003. Phytoplankton biomass from continuous plankton recorder data: an assessment of the phytoplankton colour index. J. Plankton Res. 25 (7), 697–702.

Behrenfeld, M.J., O'Malley, R.T., Siegel, D.A., McClain, C.R., Sarmiento, J.L., Feldman, G.C., Milligan, A.J., Falkowski, P.G., Letelier, R.M., Boss, E.S., 2006. Climate-driven trends in contemporary ocean productivity. Nature 444 (7120), 752–755.

Bill, B.D., 2011. Carbon and Nitrogen Uptake of Toxigenic Diatoms: *Pseudo-nitzschia australis* and *Pseudo-nitzschia turgidula*, Romberg Tiburon Center for Environmental Studies. San Francisco State University, San Francisco, California.

Bond, N.A., Cronin, M.F., Freeland, H., Mantua, N., 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. Geophys. Res. Lett. 42 (9), 3414–3420.

Bowers, H.A., Ryan, J.P., Hayashi, K., Woods, A.L., Marin, R., Smith, G.J., Hubbard, K.A., Doucette, G.J., Mikulski, C.M., Gellene, A.G., Zhang, Y.W., Kudela, R.M., Caron, D.A., Birch, J.M., Scholin, C.A., 2018. Diversity and toxicity of *Pseudo-nitzschia* species in Monterey Bay: perspectives from targeted and adaptive sampling. Harmful Algae 78, 129–141.

Boyd, P.W., Doney, S.C., 2002. Modelling regional responses by marine pelagic ecosystems to global climate change. Geophys. Res. Lett. 29 (16), 4.

Buschmann, A., Farias, L., Tapia, F., Varela, D., Vasquez, M., 2016. Red Tide Commission 2016. Final Report. p. 64. .

Capone, D.G., Hutchins, D.A., 2013. Microbial biogeochemistry of coastal upwelling regimes in a changing ocean. Nat. Geosci. 6, 711–717.

Chavez, F.P., Pennington, J.T., Castro, C.G., Ryan, J.P., Michisaki, R.P., Schlining, B., Walz, P., Buck, K.R., McFadyen, A., Collins, C.A., 2002. Biological and chemical consequences of the 1997–1998 El Niño in central California waters. Prog. Oceanogr. 54 (1-4), 205–232.

Clement, A., Lembeye, G., 1993. Phytoplankton monitoring program in the fish farming region of south Chile. In: Smayda, T.J., Shimizu, T.J. (Eds.), Toxic Phytoplankton Blooms in the Sea, pp. 223–228.

Clement, A., Aguilera, A., Fuentes, C., 2002. Análisis de marea roja en Archipiélago de Chiloé, contingencia verano 2002, XXII Congreso de Ciencias del Mar. de mayo, Valdivia, Chile, pp. 28–30.

Clement, A., Lincoqueo, L., Saldivia, M., Brito, C., Munoz, F., Fernandez, C., Perez, F., Maluje, C., Correa, N., Moncada, V., Contreras, G., 2016. Exceptional summer conditions and HABs of Pseudochattonella in Southern Chile create record impacts on salmon farms. Harmful Algae News 53, 1–3.

Cochlan, W.P., Herndon, J., Kudela, R.M., 2008. Inorganic and organic nitrogen uptake by the toxigenic diatom Pseudo—nitzschia australis (Bacillariophyceae). Harmful Algae 8, 111–118.

Condie, S.A., Oliver, E.C.J., Hallegraeff, G.M., 2019. Environmental drivers of unprecedented *Alexandrium tamarense* dinoflagellate blooms in east coast Tasmanian coastal waters, 2012-2017. Harmful Algae.

Cox, A.M., Shull, D.H., Horner, R.A., 2008. Profiles of *Alexandrium catenella* cysts in Puget Sound sediments and the relationship to paralytic shellfish poisoning events. Harmful Algae 7 (4), 379–388.

Dale, B., 2001. Marine dinoflagellate cysts as indicators of eutrophication and industrial pollution: a discussion. Sci. Total Environ. 264 (3), 235–240.

Dale, B., Edwards, M., Reid, P.C., 2006. Climate change and harmful algal blooms. In: Graneli, E., Turner, J.T. (Eds.), Ecology of Harmful Algae. Springer-Verlag, Berlin, Heidelberg, pp. 367–378.

Di Lorenzo, E., Mantua, N., 2016. Multi-year persistence of the 2014/15 North Pacific marine heatwave. Nat. Clim. Change 6 (11) 1042-+.

Ding, Q., Steig, E.J., Battisti, D.S., Wallace, J.M., 2012. Influence of the tropics on the southern annual mode. J. Clim. 25, 6330–6348.

Dorantes-Aranda, J.J., Campbell, K., Bradbury, A., Elliott, C.T., Harwood, D.T., Murray, S.A., Ugalde, S.C., Wilson, K., Burgoyne, M., Hallegraeff, G.M., 2017. Comparative performance of four immunological test kits for the detection of Paralytic Shellfish Toxins in Tasmanian shellfish. Toxicon 125, 110–119.

Du, X.N., Peterson, W., Fisher, J., Hunter, M., Peterson, J., 2016. Initiation and development of a toxic and persistent *Pseudo-nitzschia* bloom off the Oregon Coast in spring/summer 2015. PLoS One 11 (10), 17.

EASAC, 2013. Trends in Extreme Weather Events in Europe: Implications for National and European Union Adaptation Strategies. German National Academy of Sciences, Halle, Germany, pp. 1–19.

Edwards, M., Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430 (7002), 881–884.

Edwards, M., Reid, P., Planque, B., 2001. Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960–1995). Ices J. Mar. Sci. 58 (1), 39–49.

Edwards, L., Wilson, K., Veitch, M.G.K., 2018. An Outbreak of Paralytic Shellfish Poisoning in Tasmania. Communicable Diseases Intelligence, pp. 42.

Feifel, K.M., Moore, S.K., Horner, R.A., 2012. An *Alexandrium* spp. cyst record from Sequim Bay, Washington State, USA, and its relation to past climate variability. J. Phycol. 48 (3), 550–558.

Fuentes, C., Clement, A., Aguilera, A., 2006. Summer *Alexandrium* Catenella Bloom and

the Impact on Fish Farming in the XI Aysen Region, Chile, 12th International Conference on Harmful Algae. International Society for the Study of Harmful Algae (ISSHA), Copenhagen, Denmark.
Gillett, N.P., Thompson, D.W.J., 2003. Simulation of recent southern hemisphere climate change. Science 302 (5643), 273–275. https://doi.org/10.1126/science.1087440.
Gillett, N.P., Fyfe, J.C., Parker, D.E., 2013. Attribution of observed sea level pressure trends to greenhouse gas, aerosol, and ozone changes. Geophys. Res. Lett. 40, 2302–2306.
Glynn, P.W., 1984. Widespread coral mortality and the 1982-82 El Nino warming event. Environ. Conserv. 11 (2), 133–146.
Gobler, C.J., Doherty, O.M., Hattenrath-Lehmann, T.K., Griffith, A.W., Kang, Y., Litaker, R.W., 2017. Ocean warming since 1982 has expanded the niche of toxic algal blooms in the North Atlantic and North Pacific oceans. Proc. Natl. Acad. Sci. U. S. A. 114 (19), 4975–4980 Griffith and Gobler this special issue.
Grose, M.R., Barnes-Keoghan, I., Corney, S.P., White, C.J., Holz, G.K., Bennett, J.B., Gaynor, S.M., Bindoff, N.L., 2010. Climate Futures for Tasmania Technical Report – General Climate Impacts. Antarctic Climate & Ecosystems Cooperative Centre.
Guzman, L., Campódonico, I., 1975. Marea Roja en la región de Magallanes Publicaciones del Instituto de la Patagonia. Serie Monograías. Punta Arenas (Chile) N89 44 pp.
Hallegraeff, G.M., 2010. Ocean climate change, phytoplankton community responses, and harmful algal blooms: a formidable predictive challenge. J. Phycol. 46 (2), 220–235.
Hallegraeff, G.M., McCausland, M.A., Brown, R.K., 1995. Early warning of toxic dinoflagellate blooms of Gymnodinium catenatum in southern Tasmanian waters. J. Plankton Res. 17 (6), 1163–1176.
Hallegraeff, G.M., Bolch, C., Condie, S., Dorantes-Aranda, J.J., Murray, S., Quinlan, R., Ruvindy, R., Turnbull, A., Ugalde, S., Wilson, K., 2017. Unprecedented *Alexandrium* blooms in a previously low biotoxin risk area of Tasmania, Australia. In: Proenca, L., Hallegraeff, G.M. (Eds.), Proceedings of the 17th International Conference on Harmful Algae, pp. 38–41.
Hays, G.C., Richardson, A.J., Robinson, C., 2005. Climate change and marine plankton. Trends Ecol. Evol. 20 (6), 337–344.
Hickel, W., 1998. Temporal variability of micro- and nanoplankton in the German Bight in relation to hydrographic structure and nutrient changes. ICES J. Mar. Sci. 55 (4), 600–609.
IPCC, 2013. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovern-Mental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA 1535 pp.
Irwin, A.J., Finkel, Z.V., Muller-Karger, F.E., Ghinaglia, L.T., 2015. Phytoplankton adapt to changing ocean environments. Proc. Natl. Acad. Sci. U. S. A. 112 (18), 5762–5766.
John, U., Alperman, T., Nagai, S., Litaker, R.W., Murray, S., Anderson, D.M., Bolch, C., 2018. Detailed insights into *Alexandrium catenella* (Dinophyceae) (Group 1 genotype) population structure and evolution. Abstracts of the 18th Internatiional Conference on Harmful Algae, Abstract Book. p. 324.
Johnson, C.R., Banks, S.C., Barrett, N.S., Cazassus, F., Dunstan, P.K., Edgar, G.J., Frusher, S.D., Gardner, C., Haddon, M., Helidoniotis, F., Hill, K.L., Holbrook, N.J., Hosie, G.W., Last, P.R., Ling, S.D., Melbourne-Thomas, J., Miller, K., Pecl, G.T., Richardson, A.J., Ridgway, K.R., Rintoul, S.R., Ritz, D.A., Ross, D.J., Sanderson, J.C., Shepherd, S.A., Slotvvinski, A., Swadling, K.M., Taw, N., 2011. Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. J. Exp. Mar. Biol. Ecol. 400 (1–2), 17–32.
Jones, R., 1978. Why did the Tasmanians stop eating fish? In: Gould, R.A. (Ed.), Explorations in Ethnoarcheology. School of American Research and University of New Mexico Press, Albuquerque, pp. 11–14.
Jones, J.M., et al., 2016. Assessing recent trends in high-latitude Southern Hemisphere surface climate. Nat. Climate Change 6, 917–926.
Klouch, Z.K., Caradec, F., Plus, M., Hernandez-Farinas, T., Pineau-Guillou, L., Chapelle, A., Schmitt, S., Quere, J., Guillou, L., Siano, R., 2016. Heterogeneous distribution in sediments and dispersal in waters of *Alexandrium minutum* in a semi-enclosed coastal ecosystem. Harmful Algae 60, 81–91.
Kudela, R.M., Cochlan, W.P., Roberts, A., et al., 2004. Spatial and temporal patterns of *Pseudo-nitzschia* spp. in central California related to regional oceanography. In: Steidinger, K. (Ed.), Harmful Algal Blooms 2002. Intergovernmental Oceanographic Commission of UNESCO, pp. 347–349.
Kudela, R.M., Seeyave, S., Cochlan, W.P., 2010. The role of nutrients in regulation and promotion of harmful algal blooms in upwelling systems. Prog. Oceanogr. 85, 122–135.
L'Heureux, M.L., Thompson, D.W.J., 2006. Observed relationships between the El-Niño-Southern oscillation and the extratripical zonal-mean circulation. J. Clim. 19, 276–287.
Lelong, A., Hégaret, H., Soudant, P., Bates, S.S., 2012. *Pseudo-nitzschia* (Bacillariophyceae) species, domoic acid and amnesic shellfish poisoning: revisiting previous paradigms. Phycologia 51, 168–216.
Lembeye, G., Campodónico, I., 1984. First recorded bloom of the dinoflagellate *Prorocentrum micans*Ehr. in south-central Chile. Botanica Marina 27 (10), 491–493.
Lembeye, G., Marcos, N., Sfeir, A., Molinet, C., Jara, F., Clément, A., Rojas, X., 1998. Seguimiento de la toxicidad en recursos pesqueros de importancia comercial en la X y XI región. Informe Final Proyecto FIP 97, 49–86.
León-Muñoz, J., Urbina, M.A., Garreaud, R., Iriarte, J.L., 2018. Hydroclimatic conditions trigger record harmful algal bloom in western Patagonia (summer 2016). Sci. Rep. 8, 10.
Lewandowska, A.M., Hillebrand, H., Lengfellner, K., Sommer, U., 2014. Temperature effects on phytoplankton diversity – the zooplankton link. J. Sea Res. 85, 359–364.
Little, C., Felzensztein, C., Gimmon, E., Munoz, P., 2015. The business management of the Chilean salmon farming industry. Mar. Pol. 54, 108–117.
Mardones, J.I., Clement, A., 2016. Manual de Microalgas del Sur de Chile.
Mardones, J.I., Clement, A., Rojas, X., Aparicio, C., 2010. *Alexandrium catenella* during 2009 in Chilean waters, and recent expansion to coastal ocean. Harmful Algae News 41, 8–9.
Mardones, J.I., Clement, A., Rojas, X., 2012. Monitoring potentially ichthyotoxic phytoflagellates in souther fjords of Chile. Harmful Algae News 67, 6–7.
Mardones, J.I., Bolch, C., Guzman, L., Paredes, J., Varela, D., Hallegraeff, G.M., 2016. Role of resting cysts in Chilean Alexandrium catenella dinoflagellate blooms revisited. Harmful Algae 55, 238–249.
Mardones, J.I., Fuenzalida, G., Zenteno, K., Alves-de-Souza, C., Astuya, A., Dorantes-Aranda, J.J., 2019. Salinity-growth response and ichthyotoxic potency of the Chilean Pseudochattonella verruculosa. Front. Mar. Sci. 6, 24. https://doi.org/10.3389/fmars.2019.00024.
McCabe, R.M., Hickey, B.M., Kudela, R.M., Lefebvre, K.A., Adams, N.G., Bill, B.D., Gulland, F.M.D., Thomson, R.E., Cochlan, W.P., Trainer, V.L., 2016. An unprecedented coastwide toxic algal bloom linked to anomalous ocean conditions. Geophys. Res. Lett. 43 (19), 10366–10376.
McKibben, S.M., Peterson, W., Wood, M., Trainer, V.L., Hunter, M., White, A.E., 2017. Climatic regulation of the neurotoxin domoic acid. Proc. Natl. Acad. Sci. U. S. A. 114 (2), 239–244.
Moore, S.K., Mantua, N.J., Hickey, B.M., Trainer, V.L., 2009. Recent trends in paralytic shellfish toxins in Puget Sound, relationships to climate, and capacity for prediction of toxic events. Harmful Algae 8 (3), 463–477.
Moore, S.K., Mantua, N.J., Salathe, E.P., 2011. Past trends and future scenarios for environmental conditions favoring the accumulation of paralytic shellfish toxins in Puget Sound shellfish. Harmful Algae 10 (5), 521–529.
Muñoz, P., Avaria, S., Sievers, H., Prado, R., 1992. Presencia de dinoflagelados tóxicos del genero *Dinophysis* en el seno Aysén. Chile Rev. Biol. Mar. Valparaiso 27, 187–212.
NMFS, 2016. In: Commerce, U.S., Dept. of Commerce (Eds.), Fisheries of the United States, 2016. National Marine Fisheries Service.
Overland, J.E., Wang, M., 2007. In: Union, A.G. (Ed.), Future Climate of the North Pacific Ocean, pp. 178–182.
Paerl, H.W., Scott, J.T., 2010. Throwing fuel on the fire: synergistic effects of excessive nitrogen inputs and global warming on harmful algal blooms. Environ. Sci. Technol. 44 (20), 7756–7758.
Peña, M.A., Nemcek, N., Robert, M., 2018. Phytoplankton responses to the 2014-2016 warming anomaly in the northest subarctic Pacific Ocean. Limnol. Oceanogr. https://doi.org/10.1002/lno.11056. in press.
Raven et al. 2019 this issue Rebolledo, L., Lange, C.B., Bertrand, S., Muñoz, P., Salamanca, M., Lazo, P., Iriarte, J.L., Vargas, G., Pantoja, S., Dezileau, L., 2014. Late Holocene precipitation variability recorded in the sediments of Reloncaví Fjord (41°S, 72°W). Chile. Quat. Res. 84, 21–36.
Rhein, M., Rintoul, S.R., Aoki, S., Campos, E., Chambers, D., Feely, R.A., Gulev, S., Johnson, G.C., Josey, S.A., Kostianoy, A., Maruitzen, C., Roemmich, D., Talley, L.D., Wang, F., 2013. Observations: Ocean. Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Climate Change 2013: The Physical Science Basis: Contribution of Working Group I to the Fifth Assessment of the Intergovernmental Panel on Climate Change.
Ritzman, J., Brodbeck, A., Brostrom, S., McGrew, S., Dreyer, S., Klinger, T., Moore, S.K., 2018. Economic and sociocultural impacts of fisheries closures in two fishing-dependent communities following the massive 2015 U.S. West Coast harmful algal bloom. Harmful Algae 80, 35–45.
Ryan, J.P., Kudela, R.M., Birch, J.M., Blum, M., Bowers, H.A., Chavez, F.P., Doucette, G.J., Hayashi, K., Marin, R., Mikulski, C.M., Pennington, J.T., Scholin, C.A., Smith, G.J., Woods, A., Zhang, Y., 2017. Causality of an extreme harmful algal bloom in Monterey Bay, California, during the 2014-2016 northeast Pacific warm anomaly. Geophys. Res. Lett. 44 (11), 5571–5579.
Sekula-Wood, E., Benitez-Nelson, C., Morton, S., Anderson, C., Burrell, C., Thunell, R., 2011. *Pseudo-nitzschia* and domoic acid fluxes in Santa Barbara Basin (CA) from 1993 to 2008. Harmful Algae 10 (6), 567–575.
Shaw, J.L.A., Weyrich, L.S., Hallegraeff, G.M., Cooper, A., 2019. Retrospective eDNA Assessment of Harmful Algae in Historical Ship Ballast Tank and Marine Port Sediments Molecular Ecology.
Smayda, T.J., 2010. Adaptations and selection of harmful and other dinoflagellate species in upwelling systems. 2. Motility and migratory behaviour. Prog. Oceanogr. 85 (1–2), 71–91.
Smith, J., Connell, P., Evans, R.H., Gellene, A.G., Howard, M.D.A., Jones, B.H., Kaveggia, S., Palmer, L., Schnetzer, A., Seegers, B.N., Seubert, E.L., Tatters, A.O., Caron, D.A., 2018. A decade and a half of *Pseudo-nitzschia*spp. and domoic acid along the coast of southern California. Harmful Algae 79, 87–104.
Stern, R., Moore, S.K., Trainer, V.L., Bill, B.D., Fischer, A., Batten, S., 2018. Spatial and temporal patterns of *Pseudo-nitzschia* genetic diversity in the North Pacific Ocean from the Continuous Plankton Recorder survey. Mar. Ecol. Prog. Ser. 606, 7–28.
Stock, C.A., Alexander, M.A., Bond, N.A., Brander, K.M., Cheung, W.W.L., Curchitser, E.N., Delworth, T.L., Dunne, J.P., Griffies, S.M., Haltuch, M.A., Hare, J.A., Hollowed, A.B., Lehodey, P., Levin, S.A., Link, J.S., Rose, K.A., Rykaczewski, R.R., Sarmiento, J.L., Stouffer, R.J., Schwing, F.B., Vecchi, G.A., Werner, F.E., 2011. On the use of IPCC-class models to assess the impact of climate on living Marine Resources. Prog. Oceanogr. 88 (1-4), 1–27.
Swain, D.L., Langenbrunner, B., Neelin, J.D., Hall, A., 2018. Increasing precipitation volatility in twenty-first-century California. Nat. Clim. Change 8 (5) 427-+.
Tatters, A.O., Schnetzer, A., Xu, K., Walworth, N.G., Fu, F.X., Spackeen, J.L., Sipler, R.E., Bertrand, E.M., McQuaid, J.B., Allen, A.E., Bronk, D.A., Gao, K.S., Sun, J., Caron, D.A., Hutchins, D.A., 2018. Interactive effects of temperature, CO2 and nitrogen source on a coastal California diatom assemblage. J. Plankton Res. 40 (2), 151–164.
Thompson, P.A., Baird, M.E., Ingleton, T., Doblin, M.A., 2009. Long-term changes in

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temperate Australian coastal waters: implications for phytoplankton. Mar. Ecol.-Prog. Ser. 394, 1–19.
TMMC, 2015. 2015: A Year for the Record Books.
Townhill, B.L., Tinker, J., Jones, M., Potois, S., Creach, V., Simpson, S.D., Dye, S., Bear, E., Pennegar, J.K., 2018. Harmful algal blooms and climate change: exploring future distribution changes. ICES J. Mar. Sci. 75 (6), 1882–1893.
Trainer, V.L., Hickey, B.M., Lessard, E.J., Cochlan, W.P., Trick, C.G., Wells, M.L., MacFadyen, A., Moore, S.A., 2009. Variability of *Pseudo-nitzschia* and domoic acid in the Juan de Fuca Eddy region and its adjacent shelves. Limnol. Oceanogr. 54, 289–308.
Trainer, V.L., Bates, S.S., Lundholm, N., Thessen, A.E., Cochlan, W.P., Adams, N.G., Trick, C.G., 2012. Pseudo–nitzschia physiological ecology, phylogeny, toxicity, monitoring and impacts on ecosystem health. Harmful Algae 14, 271–300.
Trenberth, K.E., 2011. Changes in precipitation with climate change. Clim. Res. 47 (1-2), 123–138 2011.
Trick, C.G., Trainer, V.L., Cochlan, W.P., Wells, M.L., Beall, B.F., 2018. The successional formation and release of domoic acid in a *Pseudo-nitzschia* bloom in the Juan de Fuca Eddy: a drifter study. Harmful Algae 79, 105–114.
Venrick, E.L., 1998. Spring in the California current: the distribution of phytoplankton species, April 1993 and April 1995. Mar. Ecol. Prog. Ser. 167, 73–88.
Viale, M., Garreaud, R., 2015. Orographic effects of the subtropical and extratropical Andes on upwind precipitating clouds. J. Geophys. Res. Atmos. 120, 4962–4974.
Wang, G., Cai, W., 2013. Climate-change impact on the 20th-century relataionship between the Southern Annular Mode and global mean temperature. Sci. Rep. 3, 2039.
Wang, S.Y., Hipps, L., Gillies, R.R., Yoon, J.H., 2014. Probable causes of the abnormal ridge accompanying the 2013-2014 California drought: ENSO precursor and anthropogenic warming footprint. Geophys. Res. Lett. 41 (9), 3220–3226.
Wang, S.Y.S., Huang, W.R., Yoon, J.H., 2015. The North American winter' dipole' and extremes activity: a CMIP5 assessment. Atmos. Sci. Lett. 16 (3), 338–345.
Wasmund, N., Nausch, G., Matthaus, W., 1998. Phytoplankton spring blooms in the southern Baltic Sea – spatio-temporal development and long-term trends. J. Plankton Res. 20 (6), 1099–1117.
Wells, M.L., Trainer, V.L., Smayda, T.J., Karlson, B.S.O., Trick, C.G., Kudela, R.M., Ishikawa, A., Bernard, S., Wulff, A., Anderson, D.M., Cochlan, W.P., 2015. Harmful algal blooms and climate change: learning from the past and present to forecast the future. Harmful Algae 49, 68–93.
Whitney, F.A., 2015. Anomalous winter winds decrease 2014 transition zone productivity in the NE Pacific. Geophys. Res. Lett. 42 (2), 428–431.
Yoon, J.H., Wang, S.Y.S., Gillies, R.R., Kravitz, B., Hipps, L., Rasch, P.J., 2015. Increasing water cycle extremes in California and in relation to ENSO cycle under global warming. Nat. Commun. 6, 6.
Zhu, Z., Qu, P.P., Fu, F.X., Tennenbaum, N., Tatters, A.O., Hutchins, D.A., 2017. Understanding the blob bloom: warming increases toxicity and abundance of the harmful bloom diatom *Pseudo-nitzschia* in California coastal waters. Harmful Algae 67, 36–43.